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Primary production by marine microalage is believed to be a critical factor regulating atmospheric carbon dioxide levels and associated climatic changes. Assessments of photosynthesis in the open ocean, and the related export of organic carbon to the deep ocean (new or non-regenerative production, vary by as much as an order of magnitude (refs 2 and 6, compare with refs 3-5 and 7). Discrepancies are attributed to different temporal and spatial scales reflected by instantaneous rate measurements, as opposed to seasonally averaged measurements based on subsurface changes in chemical tracers. Satellite extrapolations of primary production can be used to characterize and quantify temporal and spatial variability. But time differentials between satellite and ship measurements as well as regional and seasonal variations in empirical relationships, have so far limited the precision of such extrapolations. We conducted extensive ship sampling of chlorophyll a and primary production in the western Mediterranean Sea contemporaneous with Nimbus-7 coastal zone colour scanner imagery. Our approach resulted

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in an empirical model for estimating integrated water-column primary production from satellite imagery. Precision was adequate to resolve short-form fluctuations in primary production associated with a mesoscale circulation feature.

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Satellite detection of transient enhanced primary production in the western Mediterranean Sea

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Primary production by marine microalgae is believed to be a critical factor regulating atmospheric carbon dioxide levels and associated climatic changes[1]. Assessments of photosynthesis in the open ocean[2–4], and the related export of organic carbon to the deep ocean (new or non-regenerative production[5–7], vary by as much as an order of magnitude (refs 2 and 6, compare with refs 3–5 and 7). Discrepancies are attributed[4,6–8] to different temporal and spatial scales reflected by instantaneous rate measurements, as opposed to seasonally averaged measurements based on subsurface changes in chemical tracers. Satellite extrapolations of primary production can be used to characterize and quantify temporal and spatial variability[9–11]. But time differentials between satellite and ship measurements, as well as regional and seasonal variations in empirical relationships, have so far limited the precision of such extrapolations[9,12]. We conducted extensive ship sampling of chlorophyll *a* and primary production in the western Mediterranean Sea contemporaneous with Nimbus-7 coastal zone colour scanner imagery. Our approach resulted in an empirical model for estimating integrated water-column primary production from satellite imagery. Precision was adequate to resolve short-term fluctuations in primary production associated with a mesoscale circulation feature.

Sampling was conducted from 5 May to 21 May 1986 aboard USNS *Lynch*, encompassing wide variations in weather and water mass characteristics. Vertical stations (Fig. 1*a*) transected density fronts that exist as a consequence of juxtaposition of Mediterranean Sea water and less saline Atlantic water entering through the Strait of Gibraltar. This Modified Atlantic Water becomes entrained in twin anticyclonic gyres in the Alboran Sea (ref. 13; R.A.A., D.A.W. and K. D. Saunders, manuscript in preparation). The flow exits the second gyre near 1° W longitude and branches eastward to form the Algerian Current[14,15]. Strong density fronts persist between Modified Atlantic Water and Mediterranean Water as far as 3° E longitude.

We examined the synoptic distribution of primary production by correlating satellite-derived surface pigment concentrations, and shipboard measurements of surface chlorophyll *a* and integrated water-column primary production. Coastal zone colour scanner (CZCS) imagery was processed[16,17] to yield surface photosynthetic pigment concentrations (C_k in mg pigments m^{-3}) using a single scattering Rayleigh model and a mid-latitude ozone absorption coefficient. The 670-nm channel was used for aerosol path removal with an epsilon value of 0.990 for the 550-nm channel. Ship estimates of surface chlorophyll *a* (C_s in mg pigments m^{-3}) were made on samples collected roughly every 6 km while the ship was underway. Samples were also collected at 5-m intervals to a depth of 100 m at the vertical stations (Fig. 1*a*). Concentrations were determined in duplicate using modifications of the methods of Smith *et al.*[18], as described by Lohrenz *et al.*[13]. Water-column primary production (π in g carbon (C) m^{-2} d^{-1}) at the vertical stations was estimated from vertical profiles of chlorophyll *a* using an empirically determined relationship between chlorophyll-specific ^{14}C-primary production and depths[13].

The relationship of water-column production (π) and surface chlorophyll *a* (C_s) at the vertical stations (Fig. 2*a*) was highly significant ($r^2 = 0.758$, $N = 39$). To develop a predictive equation for satellite extrapolation of π, individual pixel values of C_k

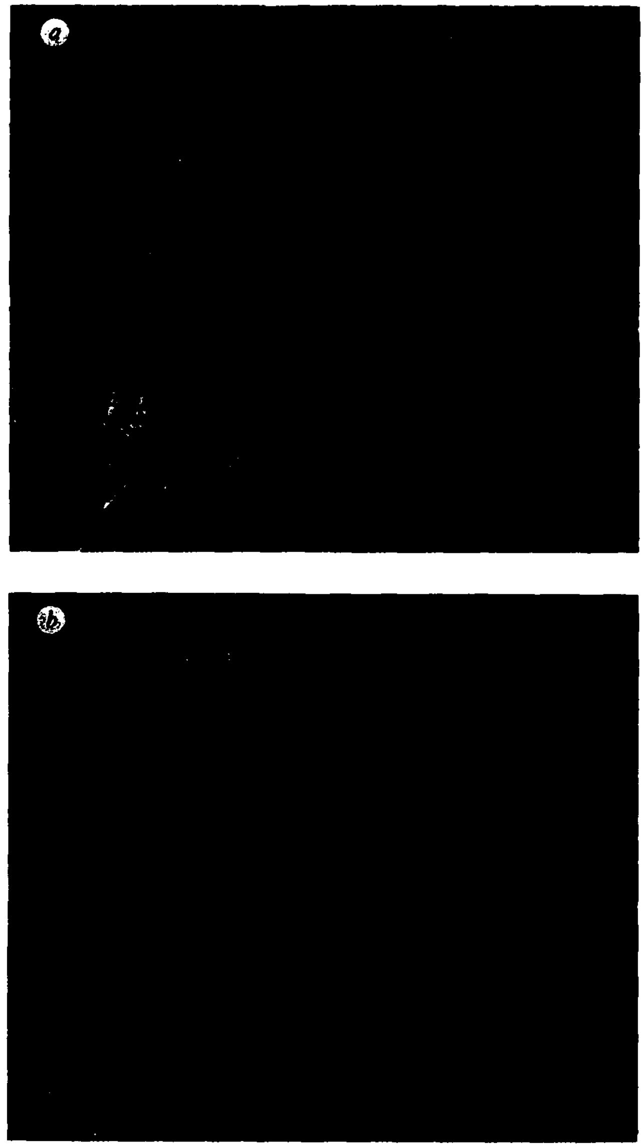

Fig. 1 CZCS images from 8 May (*a*) and 11 May (*b*) showing distribution of near-surface photosynthetic pigment concentrations (C_k in mg pigments m^{-3}) and integrated primary production (π in g C m^{-2} d^{-1}). The images have been resampled to a mercator projection such that each pixel represents 1 km^2. The order and location of ship stations are indicated by numbers in *a*. The colour scale in *b* applies to both images. Statistics in Table 1 were determined for image areas representative of the Modified Atlantic Water current (western box) and Mediterranean Water (eastern box).

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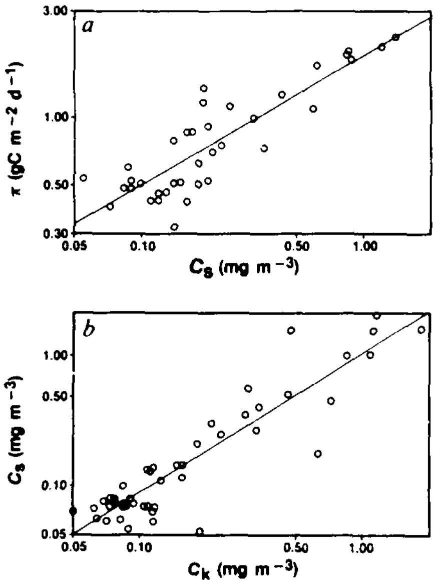

Fig. 2 *a*, log-log relationship of surface chlorophyll *a* concentration (C_s) versus integrated water-column primary production (π) determined at vertical stations. A model II regression[22] yields the equation: $\ln(\pi) = 0.633$ (±0.145, 95% confidence interval) $+ 0.579$ (±0.090) $\ln(C_s)$ (solid line). The r^2 of the correlation was 0.758 ($N = 39$). *b*, log-log relationship of CZCS-derived near-surface photosynthetic pigment concentrations (C_k) versus coincident surface chlorophyll *a* concentrations (C_s) determined from underway measurements. A model II regression gives the equation: $\ln(C_k) = 0.001$ (±0.190) $+ 0.994$ (±0.110) $\ln(C_s)$ (solid line). The r^2 of the correlation was 0.841 ($N = 48$).

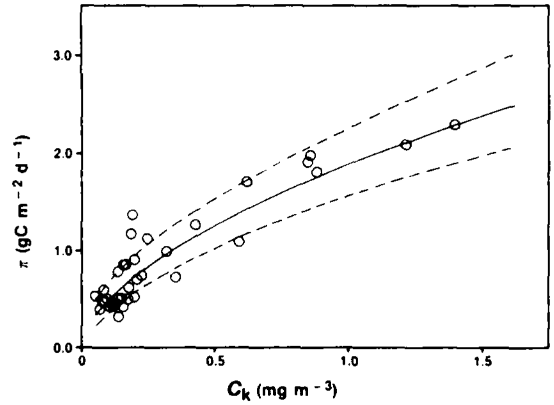

Fig. 3 Predicted integrated water-column primary production (π) based on CZCS-derived near-surface photosynthetic pigment concentrations (C_k). The predictive equation resulting from combining regression models shown in Fig. 2*a* and *b* is $\ln(\pi) = 0.634 + \ln(C_k)$ 0.576 (solid line). Dotted lines show 95% confidence limits of the prediction, propagated from errors of regressions in Fig. 2. Symbols represent the same data shown in Fig. 2*a* but replotted for comparison.

corresponding to the ship's latitude and longitude were extracted from five CZCS images (5, 8, 10, 11 and 12 May) and compared with values of C_s determined within 8 h of the satellite passing (Fig. 2*b*). The C_k versus C_s relationship was significant ($r^2 = 0.841$, $N = 48$) with a slope of 0.994 and an intercept not significantly different from zero. Although there was a persistent subsurface chlorophyll maximum[13], it occurred below the depths detected by satellite. The agreement we observed over both time and space between C_s and C_k indicates that atmospheric corrections applied to CZCS data were accurate.

A predictive model for extrapolating integrated water-column production from satellite-derived pigments (C_k) was developed by substituting the C_s term in the π versus C_s relation (Fig. 2*a*) with the equation for estimating C_s from C_k (Fig. 2*b*). The resulting relationship between π and C_k (Fig. 3) is described by the equation: $\ln(\pi) = 0.634 + 0.576 \ln(C_k)$. π and C_s data from Fig. 2*a* are replotted in Fig. 3 to illustrate the fit. Because of the extent of our ship data and its close relationship to the satellite imagery, the precision of CZCS extrapolations of π in our study is significantly improved over that of previous investigations[9-12].

We used the predictive model in Fig. 3 to extrapolate π from time-series CZCS data. CZCS images from 8 May and 11 May (Fig. 1*a* and *b* respectively) illustrate areas of higher near-surface pigment concentrations and integrated primary production associated with a current of Modified Atlantic Water (MAW) in the western Mediterranean Sea (ref. 13; R.A.A., D.A.W. and K. D. Saunders, manuscript in preparation.) The dramatic decrease in both pigment concentration and primary production from 8 May to 11 May illustrates their transient nature in that current. To quantify these changes, we selected regions on the CZCS images that were representative of relatively high (MAW, western box in Fig. 1*a* and *b*) and low (Mediterranean Water, eastern box) pigment and production levels. The statistics for the boxes are shown in Table 1 for CZCS images obtained between 30 April and 17 May 1986. In the MAW, relatively high values of π (1.8 g C m^{-2} d^{-1}) and C_k (0.9 mg pigment m^{-3}) occurred on 8 May, followed by a rapid decline. Levels increased again on 17 May. π and C_k were consistently lower for the Mediterranean Water.

The satellite interpretations provide evidence that a substantial fraction of regional production is attributable to localized and highly variable primary production events. The fronts between MAW and Mediterranean Water are sites of enhanced vertical mixing[13,19]. As nitrate concentrations were higher at depth[13,19], nitrate enrichment could thus explain the enhanced primary production observed in the MAW current, leading to the conclusion that a significant proportion of total production is new production in that area.

Recognition and characterization of transient primary production events in other nutrient-limited regimes may help to

Table 1 Time series of satellite-estimated integrated water-column primary production (π) and near-surface pigments (C_k)

	Modified Atlantic Water			Mediterranean Water		
Date	π (g C m^{-2} d^{-1})	C_k (mg m^{-3})	CV (%)	π (g C m^{-2} d^{-1})	C_k (mg m^{-3})	CV (%)
30 April	1.2	0.45	15	0.5	0.11	21
8 May	1.8	0.90	19	0.6	0.13	14
11 May	0.8	0.25	14	0.5	0.11	16
12 May	0.6	0.15	17	0.3	0.05	91
17 May	1.9	1.10	15	—	clouds	—

Estimates were determined for areas representative of the Modified Atlantic Water current and Mediterranean Water (western and eastern boxes in Fig. 1 respectively). Means and coefficients of variation (CV) were determined for pixel values before converting to π and C_k. Area in km^2 (and number of pixels) was 1,996 for modified Atlantic Water and 2,141 for Mediterranean Water boxes. Representative attenuation lengths were determined using a spectral radiometer[21] and were 15 m for Mediterranean and 13 m for Modified Atlantic Water types.

resolve discrepancies between integrated synoptic-scale tracer measurements and discrete instantaneous rate measurements. Jenkins[7] suggested that a major source of nitrate flux in the North Atlantic Ocean may result from nutrient injection events associated with mesoscale features. Whereas subsurface tracer measurements[3-5,7] must infer such pulses from long-term averaged data, satellite imagery provides the ability to examine transients in near real-time. Closer coordination of upper ocean measurements and remote sensing research[20] should lead to more precise estimates of primary production and an improved understanding of contributions of marine biogeochemical cycles to global scale processes.

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